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A NEW ATTEMPT TO CONSTRUCT LIFE TABLES FOR KENT ISLAND HERRING GULLS

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No. 11—*A New Attempt to Construct Life Tables for Kent Island Herring Gulls*[1]

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RAYMOND A. PAYNTER, JR.

INTRODUCTION

An earlier attempt (Paynter, 1949) to construct a life table for the population of Herring Gulls (*Larus argentatus smithsonianus*) on Kent Island, New Brunswick, yielded results which seemed in conflict with the observed status of the colony. The life table indicated that the population was in a steep decline, although the size of the colony was thought to be constant or possibly even producing a population surplus which was contributing to the general increase in Herring Gulls that had been noted in northeastern North America for nearly half a century. To account for the discrepancy between the life table and what was believed to be the actual status of the population, it was suggested that, (1) the 1935 class (erroneously cited as "1936"), which was utilized to construct the postfledging portion of the table, had been banded too short a time (11 years) to yield all potential recoveries, thereby producing a truncated table; (2) that the 1935 year class may have suffered unusually severe postfledging mortality or that the 1947 year class, which provided data for the egg and nestling portion of the table, may also have been unrepresentative, or possibly both situations had prevailed; (3) that there may have been a loss of bands, particularly among older birds, that caused the calculated survival rate and life expectancy to be lowered.

Fifteen years have elapsed since that study. Additional birds from the 1935 class have been recovered and it is now possible to test the hypothesis that older recoveries might be sufficient to raise the calculated life expectancy and survival rates to levels commensurate with the presumed status of the population. Recoveries from bandings in other years at Kent Island have also accumulated, allowing comparisons between several year classes. Finally, there have been published three additional life tables for the species (Paludan, 1951; Hickey, 1952; Olsson, 1958) and these provide valuable comparative data. It is the purpose of this

[1] Contribution No. 32 from the Bowdoin Scientific Station, Kent Island, Grand Manan, New Brunswick, Canada.

paper to re-examine the dynamics of the Kent Island Herring Gull population in the light of these developments.

MATERIAL AND METHODS

In calculating ages of banded gulls it has been the custom at Kent Island (e.g., Paynter, 1947; 1949) to begin the year on July first, which is about the earliest chicks are large enough to band. To avoid the inclusion of prefledging mortality in the banding recoveries, bands were removed from any chicks dying before fledging and were placed on other young.

In some banding studies it is necessary to make adjustments for bias resulting from the disproportionate recovery of newly fledged birds in the vicinity of their place of birth (see Farner, 1955). This correction is not required of the Kent Island data because the gulls leave the island shortly after they are able to fly and disperse over a wide area (Gross, 1940) where, presumably, they are no more likely to be recovered than older birds.

Banding began at Kent Island in 1934. The terminal date for data used in this study is 30 June 1963. Thus, the oldest potential recovery would be a bird in its twenty-eighth year. To date the oldest record of a gull banded as a fledgling is an individual caught at Kent Island in its twenty-sixth year and released bearing a new band. The oldest record of a bird dying while still wearing its original band is a gull in its twenty-fourth year; the next oldest is a twenty-second year bird. For purposes of this study only young banded in the six year classes from 1934 through 1939 will be considered. The maximum potential age for birds in the most recently banded year class is twenty-three years, which seems close to the maximum age of recovery that may be expected in the Kent Island population (see p. 514). A few birds older than twenty-six almost certainly will be found in future years, but they probably play an insignificant part in the dynamics of this population.

Heeding Hickey's warnings (1952) of clerical and other errors in the banding records kept by the Fish and Wildlife Service, microfilms of all Kent Island banding schedules and recovery records were obtained through the courtesy of Allen J. Duvall. These were carefully compared with the files at Kent Island and all erroneous and questionable data were eliminated. I have no illusions about the complete accuracy of the resulting material, but considering the fact that hundreds of people have been involved in reporting and handling these data during three decades, no further refinements seem possible. It is believed that the quantity of data is sufficient to offset whatever deficiencies in quality remain.

TABLE I

Kent Island Fledglings Banded and Admissible[1] Recoveries

Year	Banded	Recoveries	Per cent
1934	3,646	125	3.43
1935	10,748	352	3.27
1936	6,665	254	3.81
1937	4,652	146	3.14
1938	2,983	77	2.58
1939	3,000	145	4.83
Total	31,694	1,099	3.47

[1] See below for definition of admissible recoveries.

From 1934 through 1939 nearly 32,000 fledgling gulls were banded on Kent Island (Table I). Discrepancies between the yearly totals in Table I and those published previously (Paynter, 1947) result from the re-analysis of the Fish and Wildlife Service records.

These 32,000 bandings have yielded 1,206 recoveries and returns. It is necessary, however, to remove from consideration records in certain categories. Because the Kent Island life table is to be constructed from a mortality series, no records of living birds ("returns") are admissible. As a consequence, those individuals which were trapped in later years at Kent Island and found bearing bands are eliminated, as are those birds which were reported to the Fish and Wildlife Service as having been "captured and released." On the grounds of uncertainty, whether the banded bird was living or dead, Hickey (1952, p. 94) probably would exclude those records reporting "no information," "observed," "found ill," "caught by fisherman," etc. Some of these reports doubtless pertain to gulls not yet dead when their bands were read, but it seems unlikely that many of these records could have been obtained from birds that were not already weakened from illness or injury and soon to die. For this reason I include these records in the mortality series.

Also eliminated from the study are gulls collected in connection with research at Kent Island and those shot elsewhere under gull control permits. Neither of these hazards operated consistently from year to year.

Lack (1954, p. 91) notes that the inclusion of birds which have been recovered by means of shooting (i.e. "normal" shooting — not systematic control) may introduce bias if this category represents a substantial portion of the recovery sample and if juveniles are more easily shot than adults. In certain instances this may be correct, but if a given cohort is hunted with equal intensity throughout its life span, shooting must be considered to be merely another one of the hazards acting upon a population, such as the stress of weather and the toll of predators. The fact that young birds may be more easily shot than older ones does not bias the sample any more than does the fact that adverse weather or predators may claim more young than adults. On the other hand, banded birds which are shot, or for that matter killed through any human agency, probably are more likely to be reported than birds dying of disease or other natural causes. Human activity, therefore, may appear as a disproportionately high cause of death in the sample of recoveries and may also increase the total number of recoveries. But, as long as the human activity causing death operates consistently throughout the life of a cohort, the recoveries need not be excluded from the mortality series used in preparing a life table.

About five per cent of all Kent Island recoveries are of individuals reported as shot; the true rate is probably higher but, because the species is protected by law, is concealed within the reports as "found," "no information," etc. The actual percentage is certainly not nearly so high as in Europe, where the species is unprotected and where about 60 per cent of all reports are of gulls which have been shot (Paludan, 1951; Olsson, 1958). There is no reason to suspect that the distribution by age or year class of recoveries of Kent Island gulls shot but reported in other categories differs from that of birds accurately recorded as shot. Taking the shooting reports at face value, we find considerable variation in the percentage of these recoveries within various age classes, as well as within year classes. For example, in the 1935 cohort, about 6.5 per cent of the gulls were reported as shot; there were no records of birds shot beyond their seventh year and the percentages of reports from the first year through the seventh year are 8.4, 2.9, 6.5, 4.1, 16.0, 0, and 5.2. In contrast, in the 1936 year class, only 3.6 per cent of the records are of birds shot; the oldest was in its twelfth year and the percentages by age classes run 4.8, 3.0, 0, 0, 5.2, 0, 0, 0, 0, 50.0, 0, and 50.0. The distribution of shooting reports illustrated here is similar in all six cohorts. It is of interest that while shooting occurs only in the first half of the maximum potential life span (there are no records beyond the thirteenth year), there is no clear-cut pattern within this period. One might have expected to find shooting relatively more common among immature (and inexperienced) birds.

Birds recovered after having been rebanded are excluded. If Kent Island gulls lose bands, which they doubtless do, and if the loss is a function of the age of the bands rather than a random occurrence throughout the life span of the birds, this may be evident in the life table, provided it is not obscured by other phenomena, as a declining survival rate. The inclusion of rebanded birds in the study, while possibly giving a truer picture of age-specific survival rates, would introduce another source of bias. Unfortunately, there has been an insufficient number of rebandings to allow an analysis of birds in this category.

The Kent Island life tables are begun with the laying of the first egg, which occurs in late May, roughly one-tenth of a year earlier than the July 1 date taken as the start of the year when calculating the ages of banded birds. Because there were no studies of the survival of the eggs and chicks at Kent Island during the period 1934-1939, the records of the 1947 year class (Paynter, 1949) are used, creating composite tables. The mean incubation period is taken at 28 days, or 0.07 years. In 1947 it was found that 28.6 per cent of the eggs failed to hatch; the mean age of the young at fledging was calculated to be 43 days (0.12 years), and 48.5 per cent of the chicks are believed to have failed to fledge, giving a production of 0.92 fledglings per breeding pair.

KENT ISLAND LIFE TABLES

Composite life tables, using the 1947 prefledging data, for the six-year classes from 1934 through 1939, as well as a table for the combined year classes, are presented in Table II. Semi-logarithmic survivorship curves (l_x) are shown in Figures 1 and 2.

The table and graph for the combined six-year classes (Table II; Fig. 2) indicate that about 63 per cent of the eggs laid fail to produce fledged young (see Paynter, 1949, for discussion). Then there is heavy mortality (45 per cent) from the time of fledging until the following July 1, a somewhat lessened rate for the second year of life (35 per cent), and finally a lower average rate for the bulk of the remaining life span (26.8 per cent for the years 3 through 15). This is the expected pattern for most long-lived avian populations. It suggests that young (post-fledging) gulls are less able to cope with the hazards of their environment and that birds surviving the first two years of life have either learned to avoid more of the hazards, or the less adept ones have been eliminated through natural selection. If data for the oldest age groups were more abundant one might find the mortality rate increasing because of the senility. On the other hand, it is unlikely many animals survive this long in nature and that we shall ever have sufficient data from senile individuals to document this phenomenon, if indeed it does occur.

Examined individually, the life tables and survivorship curves (Table II; Fig. 1) show interesting similarities as well as differences, which one expects of natural populations in a variable environment. For example, in four of the six cohorts the mortality rate declined the year following fledging, but in the 1936 and 1938 year classes it rose. The first year postfledging mortality rate for the 1936 cohort was 36.2 per cent, which is unusually low and as a result was slightly below the rate of the second year (39.5 per cent), which was only a little in excess of the average (35 per cent). The same pattern was displayed, in a more exaggerated manner, in the 1938 cohort. The mortality rate in the first year was a comparatively low 37.7 per cent, but in the second year it jumped to 52.1 per cent, the highest observed. Similar yearly fluctuations occur throughout the life tables. Annual variations in the severity of the weather are presumably responsible for many of these swings, but the problem has not been studied.

Next to be considered is the reproductive potentiality of the colony as indicated by the life tables. North American gulls are assumed to breed in their fourth year (year 3-4) or, in other words, three summers after hatching. This may not be an exact assumption for Drost, Focke, and Freytag (1961) found in a German colony of European Herring Gulls (*L. a. argentatus*) that 20 per cent bred in their third year, 25 per cent in their fourth year, and 55 per cent in their fifth year, with the mean breeding age slightly in excess of four years. Paludan (1951), however, concluded that Danish gulls regularly breed in their third year, basing this on a single observation of a bird of this age in a breeding colony. The gull had some dark areas on the tail and on the lesser wing coverts. From this Paludan assumed that fully adult plumage is attained in the third year and that

TABLE II

Composite Life Tables for Kent Island Cohorts 1934-1939, Utilizing 1947 Prefledging Mortality Data of Paynter (1949)

1934 Cohort

x	l_x	d_x	$1{,}000q_x$	e_x
Age in years	No. surviving to start of age interval out of 1,000 eggs laid	No. dying in age interval out of 1,000 eggs laid	Mortality rate per 1,000 alive at start of age interval	Expectation of life remaining to those attaining the age interval (in years)
0.00-0.07	1,000.0	286.0	286.0	.97
0.07-0.19	714.0	346.3	485.0	1.28
0.19-1.10	367.7	182.4	496.1	2.31
1.10-2.10	185.3	44.1	238.0	3.23
2.10-3.10	141.2	26.5	187.7	3.09
3.10-4.10	114.7	20.1	175.2	2.68
4.10-5.10	94.6	38.4	405.9	2.15
5.10-6.10	56.2	23.7	421.7	2.28
6.10-7.10	32.5	11.8	363.1	2.57
7.10-8.10	20.7	8.9	429.9	2.76
8.10-9.10	11.8	0	0	3.47
9.10-10.10	11.8	3.0	254.2	2.47
10.10-11.10	8.8	3.0	340.9	2.14
11.10-12.10	5.8	0	0	1.98
12.10-13.10	5.8	2.9	500.0	.98
13.10-14.10	2.9	2.9	1,000.0	.50

1935 Cohort

x	l_x	d_x	$1{,}000q_x$	e_x
0.00-0.07	1,000.0	286.0	286.0	.94
0.07-0.19	714.0	346.3	485.0	1.23
0.19-1.10	367.7	176.5	480.0	2.21
1.10-2.10	191.2	70.0	366.1	2.92
2.10-3.10	121.2	30.3	250.0	3.33
3.10-4.10	90.9	23.0	253.0	3.27
4.10-5.10	67.9	20.9	307.8	3.21
5.10-6.10	47.0	13.6	289.4	3.41
6.10-7.10	33.4	10.5	314.4	3.60
7.10-8.10	22.9	4.2	183.4	4.02
8.10-9.10	18.7	4.2	224.6	3.81
9.10-10.10	14.5	2.1	144.8	3.76
10.10-11.10	12.4	2.1	169.3	3.32
11.10-12.10	10.3	4.1	398.1	2.90
12.10-13.10	6.2	1.0	161.3	3.50
13.10-14.10	5.2	2.1	403.8	3.08
14.10-15.10	3.1	1.0	322.6	3.84
15.10-16.10	2.1	0	0	4.43
16.10-17.10	2.1	0	0	3.38
17.10-18.10	2.1	1.1	523.8	2.38
18.10-19.10	1.0	0	0	3.50
19.10-20.10	1.0	0	0	2.50
20.10-21.10	1.0	0	0	1.50
21.10-22.10	1.0	1.0	1,000.0	.50

1936 Cohort

x	l_x	d_x	1,000 q_x	e_x
0.00-0.07	1,000.0	286.0	286.0	1.04
0.07-0.19	714.0	346.3	485.0	1.38
0.19-1.10	367.7	133.1	362.0	2.50
1.10-2.10	234.6	92.7	395.1	2.75
2.10-3.10	141.9	39.2	276.2	3.23
3.10-4.10	102.7	23.1	224.9	3.27
4.10-5.10	79.6	27.5	345.5	3.07
5.10-6.10	52.1	18.8	360.8	3.42
6.10-7.10	33.3	8.7	261.3	4.08
7.10-8.10	24.6	4.4	178.9	4.35
8.10-9.10	20.2	5.8	287.1	4.19
9.10-10.10	14.4	2.9	201.4	4.68
10.10-11.10	11.5	1.4	121.7	4.74
11.10-12.10	10.1	2.9	287.1	4.33
12.10-13.10	7.2	1.4	199.4	4.87
13.10-14.10	5.8	1.5	258.6	4.93
14.10-15.10	4.3	0	0	5.49
15.10-16.10	4.3	1.4	325.6	4.56
16.10-17.10	2.9	0	0	5.41
17.10-18.10	2.9	0	0	4.41
18.10-19.10	2.9	0	0	3.41
19.10-20.10	2.9	1.5	517.2	2.41
20.10-21.10	1.4	0	0	3.50
21.10-22.10	1.4	0	0	2.50
22.10-23.10	1.4	0	0	1.50
23.10-24.10	1.4	1.4	1,000.0	.50

1937 Cohort

x	l_x	d_x	1,000 q_x	e_x
0.00-0.07	1,000.0	286.0	286.0	.85
0.07-0.19	714.0	346.3	485.0	1.10
0.19-1.10	367.7	176.5	480.0	1.96
1.10-2.10	191.2	52.8	276.1	2.45
2.10-3.10	138.4	37.8	273.1	2.19
3.10-4.10	100.6	22.6	224.6	1.83
4.10-5.10	78.0	30.2	387.2	2.24
5.10-6.10	47.8	20.1	420.5	2.34
6.10-7.10	27.7	5.0	180.5	2.68
7.10-8.10	22.7	10.1	445.0	2.16
8.10-9.10	12.6	0	0	2.50
9.10-10.10	12.6	5.0	396.8	1.50
10.10-11.10	7.6	2.5	328.9	1.16
11.10-12.10	5.1	5.1	1,000.0	.49

1938 Cohort

x	l_x	d_x	$1,000\,q_x$	e_x
0.00-0.07	1,000.0	286.0	286.0	.89
0.07-0.19	714.0	346.3	485.0	1.16
0.19-1.10	367.7	138.6	376.9	2.09
1.10-2.10	229.1	119.4	521.2	2.16
2.10-3.10	109.7	33.4	304.5	2.97
3.10-4.10	76.3	14.3	190.0	3.06
4.10-5.10	62.0	9.6	154.8	2.65
5.10-6.10	52.4	19.1	364.5	2.04
6.10-7.10	33.3	9.5	285.3	1.92
7.10-8.10	23.8	9.5	399.2	1.50
8.10-9.10	14.3	4.8	335.7	1.16
9.10-10.10	9.5	9.5	1,000.0	.49

1939 Cohort

x	l_x	d_x	$1,000\,q_x$	e_x
0.00-0.07	1,000.0	286.0	286.0	1.04
0.07-0.19	714.0	346.3	485.0	1.38
0.19-1.10	367.7	182.8	497.1	2.49
1.10-2.10	184.9	71.0	384.0	3.60
2.10-3.10	113.9	32.0	280.9	4.54
3.10-4.10	81.0	10.1	124.7	5.18
4.10-5.10	70.9	12.7	179.1	4.85
5.10-6.10	58.2	7.6	130.6	4.79
6.10-7.10	50.6	7.6	150.2	4.44
7.10-8.10	43.0	7.6	176.7	4.13
8.10-9.10	35.4	2.5	70.6	3.91
9.10-10.10	32.9	7.6	231.0	3.18
10.10-11.10	25.3	5.1	201.6	2.98
11.10-12.10	20.2	7.6	376.2	2.61
12.10-13.10	12.6	0	0	2.88
13.10-14.10	12.6	7.6	603.1	1.88
14.10-15.10	5.0	2.5	500.0	2.98
15.10-16.10	2.5	0	0	4.48
16.10-17.10	2.5	0	0	3.48
17.10-18.10	2.5	0	0	2.48
18.10-19.10	2.5	0	0	1.48
19.10-20.10	2.5	2.5	1,000.0	.48

Combined 1934-1939 Cohorts

x	l_x	d_x	1,000 q_x	e_x
0.00-0.07	1,000.0	286.0	286.0	.95
0.07-0.19	714.0	346.3	485.0	1.25
0.19-1.10	367.7	165.5	450.1	2.26
1.10-2.10	202.2	71.7	354.6	2.82
2.10-3.10	128.5	33.4	260.0	3.27
3.10-4.10	95.1	20.4	214.5	3.30
4.10-5.10	74.7	23.7	317.3	3.07
5.10-6.10	51.0	15.3	300.0	3.26
6.10-7.10	34.7	9.0	259.4	3.56
7.10-8.10	25.7	6.4	249.0	3.63
8.10-9.10	19.3	3.3	171.0	3.67
9.10-10.10	16.0	4.0	250.0	3.33
10.10-11.10	12.0	2.4	200.0	3.27
11.10-12.10	9.6	3.6	375.0	2.95
12.10-13.10	6.0	1.0	166.7	3.43
13.10-14.10	5.0	2.3	460.0	3.02
14.10-15.10	2.7	.7	259.3	4.18
15.10-16.10	2.0	.3	150.0	4.50
16.10-17.10	1.7	0	0	4.23
17.10-18.10	1.7	.3	176.5	3.23
18.10-19.10	1.4	0	0	2.86
19.10-20.10	1.4	.7	121.4	1.86
20.10-21.10	.7	0	0	2.29
21.10-22.10	.7	.4	571.4	1.28
22.10-23.10	.3	0	0	1.33
23.10-24.10	.3	.3	1,000.0	.33

the bird was merely retarded. This appears to be an unnecessarily complicated interpretation. It would seem more logical to conclude that this was a case of an early breeder. Lacking data for the Kent Island gulls, we shall accept the fourth year as the mean breeding age.

In 1947 the average clutch size at Kent Island was nearly 2.5 eggs (Paynter, 1949). Observations (unpublished) in 1948 indicated a somewhat higher mean for first clutches (ca. 2.75) and a lower mean (ca. 2.00) for clutches replacing those lost through predation, but the average for all final clutches was again close to 2.5 eggs.

Taking the life table for the combined years 1934-1939, we find that from an initial cohort of 1,000 eggs 95.1 birds survive to July 1 of the third summer after hatching. It will be recalled that July 1 is the time when banding of the chicks is first practical and that egg-laying begins about one-tenth of a year earlier, in late May. We must, therefore, take into account birds which are alive at the time of laying but which do not survive until July 1. From the life table it is seen that 33.4 birds die during the third year. If the mortality rate is constant throughout the year, one-tenth, or 3.3 birds, die between the time of laying and the first of July. These individuals may then be added to those alive on July 1, giving a total of 98.4 birds which survive to breed for the first time from 1,000 eggs laid four summers earlier.

If the sex ratio is equal, and there is no evidence that it is not, there is an average of 49.2 pairs alive at the start of the first breeding season. At this point these birds have a mean life expectancy of about 3.3 years. If they breed annually, which they probably do for the greater part of their life spans, and lay a yearly average of 2.5 eggs per clutch, the 49.2 pairs are capable of producing 405.9 eggs. This is only 41 per cent of the number required to maintain a stable population.

The only year class with a life table differing materially from the combined 1934-1939 table is the 1939 cohort, with its generally better survival rate among older birds. The calculated number of birds at the start of the first breeding season is 84.2. The mean life expectancy is about 5.2 years. This would allow for a lifetime production of approximately 547 eggs, which again is still far short of the 1,000 eggs needed for a stable population.

If these life tables accurately represent the dynamics of the Kent Island population, it is obvious that the size of the colony should have been rapidly declining in the 1930's and early 1940's, and that the magnitude of the decline would be so great that it would be apparent to field observers. Only constant, large-scale immigration could obscure this phenomenon. Unfortunately, the colony was not accurately censused until 1940 (Crystal, 1941), when approximately 12,000 nests were counted, and the presence of 3,000 more was estimated. Allowing for the inclusion of "play nests" (Goethe, 1937), there must have been a breeding population well in excess of 20,000 birds. During my field work from 1946 through 1948 the colony was densely populated and I estimated it to contain 25,000 to 30,000 individuals (Paynter, 1949). The late Ernest Joy informed me that he had noticed no change in the size of the colony during his tenure as warden from 1935 to 1948. Thus, we must conclude that the Kent Island population was stable, or at least not noticeably unstable, from at least 1935 through 1948. The possibility remains that the colony was failing to reproduce itself and was dependent

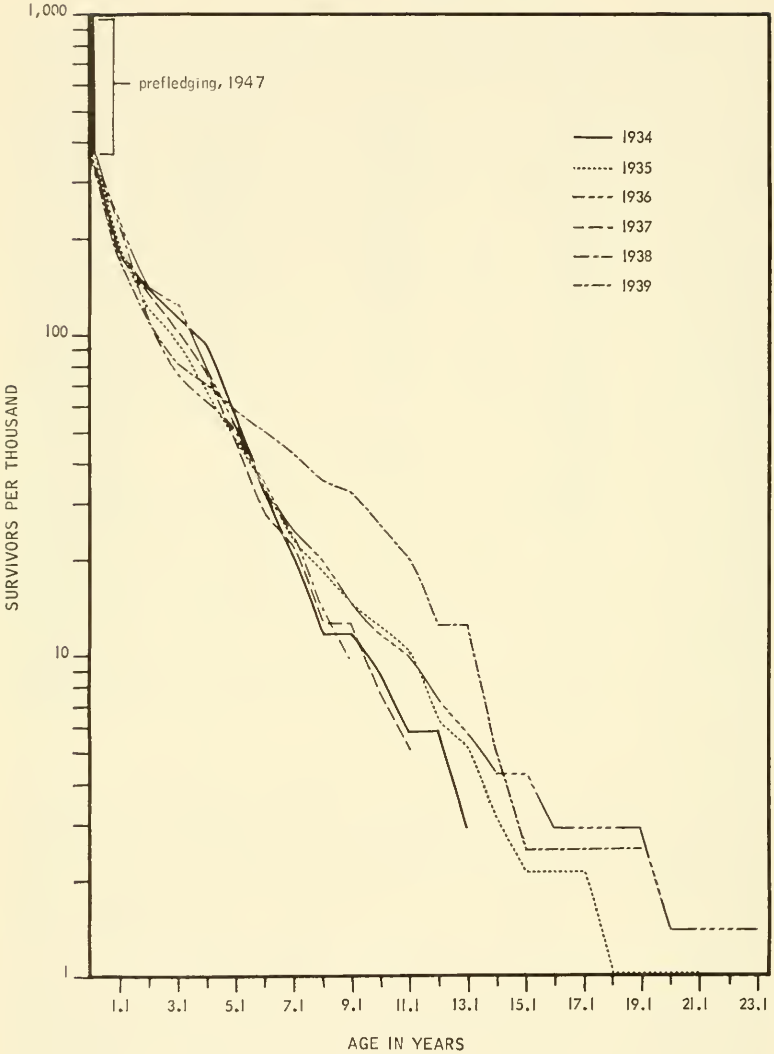

FIG. 1. Survivorship curves for Kent Island cohorts 1934-39.

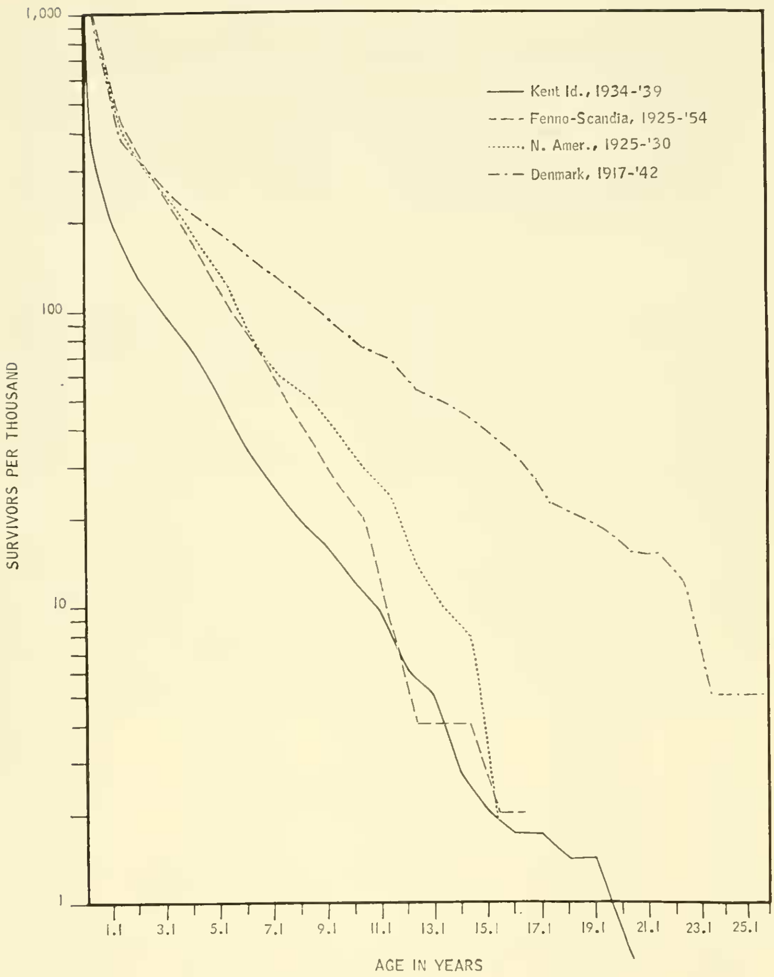

FIG. 2. Survivorship curves for four populations.

on immigrants to maintain a constant size, but this seems improbable. The Herring Gull has been increasing along the eastern seaboard, as well as in Europe, since the turn of the century. It would appear unlikely that the Kent Island colony was not contributing to this general increase. A more reasonable conclusion is that the six life tables are deficient. Before speculating on the possible reasons for this, life tables for other populations of the species will be examined.

OTHER LIFE TABLES

Hickey (1952) has considered the first three life tables prepared for North American Herring Gulls (viz., Marshall, 1947; Paynter, 1947, 1949), commenting on their errors and discrepancies; they need not be reconsidered here. Then using recoveries of gulls banded at various colonies in North America from 1925 through 1930, Hickey constructed an abridged life table for a

TABLE III

Life Table for Theoretical Population of North American Gulls Banded 1925-1930 (504 Recoveries) (after Hickey, 1952)

x	l_x	d_x	$1,000\ q_x$	e_x
0–1	1,000.0	599.2	599.2	2.00
1–2	400.8	117.1	292.1	3.25
2–3	283.7	59.5	209.7	3.39
3–4	224.2	61.5	274.3	3.15
4–5	162.7	41.7	256.2	3.16
5–6	121.0	45.6	376.8	3.08
6–7	75.4	16.1	213.5	3.63
7–8	59.3	7.9	133.2	3.48
8–9	51.4	11.9	231.5	2.95
9–10	39.5	9.9	250.6	2.69
10–11	29.6	5.9	199.3	2.42
11–12	23.7	9.9	417.7	1.90
12–13	13.8	4.0	289.8	1.91
13–14	9.8	2.0	204.1	1.48
14–15	7.8	5.9	756.4	.73
15–16	1.9	1.9	1,000.0	.47

theoretical population of 504 birds, beginning the table with reports received subsequent to 31 August of the year in which the gulls were hatched. No reports were available for gulls older than their sixteenth year. Although the table is probably foreshortened, recoveries beyond the sixteenth year are so infrequent that the resulting table is doubtless close to what would have been found if it had not been terminated until all potential recoveries had been obtained. Adjustments were made for yearly variations in the number of birds banded and for the fact that some birds had not been banded sufficiently long to yield recoveries in the year 15-16 (see Hickey, 1952, p. 11). This life table, recalculated to form a cohort of 1,000, is presented in Table III, and the survivorship curve is plotted in Figure 2.

The first year mortality rate is about 60 per cent, in contrast to an average of 45 per cent at Kent Island from the time of fledging in August to the following June 30, and the second year mortality is 29 per cent, compared to the Kent Island figure of 35.5 per cent. The mean annual mortality rate for the next ten years is 25.6 per cent, which is almost exactly that at Kent Island (Table IV).

Because this table is begun in September, neglecting the egg, nestling, and earliest postfledging mortality, a different technique from that used with the Kent Island data must be employed to assess the reproductive potential of the population.

TABLE IV

Mean Mortality Rates

Population	Age		
	0-1	1-2	2-12
Kent Id., 1934-'39	45.0[1]	35.5	26.0
North Amer. (Hickey, 1952)	59.9[2]	29.2	25.6
Denmark (Paludan, 1951)	62.3[2]	21.7	15.6
Fenno-Scandia (Olsson, 1958)	56.8[3]	31.9	33.8

[1]First interval 0.9 year, i.e. fledging to 30 June following year; 1 July to 30 June thereafter.

[2]Year begins 1 September.

[3]Year begins 1 August.

This is done by totaling the l_x column (survivors) from the year 3-4 (first breeding year) to the end of the table, dividing the total by two to give the number of pairs of breeding birds, and, finally, dividing the initial cohort (1,000) by the number of pairs of breeding birds (see Hickey, 1952, pp. 94-95). The result is the average number of young per pair of adults which need be raised to the first of September of the year of hatching in order to maintain a stable population. Applying this to Hickey's table, we find that an average of 2.44 young must be fledged and survive to September 1. This is only slightly below the mean clutch size found at Kent Island (2.5) and, therefore, allows almost no egg or chick mortality. Even if the mean clutch is assumed to be three, which is the maximum number of eggs laid by Herring Gulls, except for an exceedingly rare clutch of four (about 0.6 per cent of all clutches [Paludan, 1951, p. 49]), this would also allow for but 19 per cent mortality between the laying of the first egg and September 1. Such a mortality rate seems much too low in the light of observations at Kent Island, where more than 60 per cent of the eggs failed to yield fledged young. This life table cannot, therefore, be accepted.

The first life table for a European population of Herring Gulls is that constructed by Paludan (1951) for 966 recoveries, including those shot (ca. 60 per cent). from 11,689 birds banded in Denmark from 1917 through 1942 (Table V). The oldest recovery is that of an individual in its twenty-sixth year; the oldest potential recovery at the time the table was compiled would have been a thirty-fourth year bird. Adjustments, similar to those of Hickey (1952), were made to compensate for the fact that only 8 of the 26 year classes had been banded sufficiently long to yield recoveries in the twenty-sixth year. The mean recovery rate for these eight cohorts was 8.54 per cent, versus only 3.47 per cent for the six cohorts at Kent Island. The marked difference in recoveries is doubtless due to the frequency with which Danish gulls are shot, which enhances the chances that a banded bird will be reported, and also probably due to a better retention of bands, which will be considered subsequently. From this table (Table V), which starts on September 1 following hatching, it is seen that the first year mortality is 62.3 per cent, closely approximating Hickey's finding in North America. The second year mortality drops to 21.7 per cent, which is considerably lower than that in Hickey's table (29.2 per cent) or the Kent Island table (35.5 per cent). The mean annual mortality for the next ten years is only 15.6 per cent, in contrast to the North American

TABLE V
Life Table for Danish Gulls Banded 1917-1942 (966 Recoveries) (Paludan, 1951)

x	l_x	d_x	$1{,}000\ q_x$	e_x
0-1	1,000	623	623	2.72
1-2	377	82	217	5.39
2-3	295	56	190	5.75
3-4	239	37	155	5.98
4-5	202	28	129	5.98
5-6	174	30	172	5.83
6-7	144	18	125	5.95
7-8	126	21	167	5.73
8-9	105	17	162	5.79
9-10	88	14	159	5.83
10-11	74	6	81	5.84
11-12	68	15	221	5.35
12-13	53	4	75	5.68
13-14	49	6	122	5.12
14-15	43	7	163	4.72
15-16	36	6	167	4.56
16-17	30	8	267	4.42
17-18	22	2	91	4.96
18-19	20	2	100	4.37
19-20	18	3	167	3.81
20-21	15	0	0	3.37
21-22	15	3	200	2.37
22-23	12	7	583	1.83
23-24	5	0	0	2.50
24-25	5	0	0	1.50
25-26	5	5	1,000	0.50

and Kent Island rates of about 26 per cent (Table IV). This low rate gives a survivorship curve (Fig. 2) which is strikingly different, after the second year, from those of the Kent Island and North American populations.

Applying the same methods for determining the required productivity of this population as were used with Hickey's data, it is found that to maintain a constant population it is necessary for a pair of gulls to raise 1.3 young to September first following hatching. While this would necessitate about 40 per cent greater productivity than recorded (Paynter, 1949) at Kent Island (0.92 young per pair raised to fledging in early August), it may be a reasonable expectation. On the other hand, the prefledging mortality in Paludan's colony was considerably higher than that at Kent Island. In the Danish colony in 1943 there was about a 10 per cent loss of eggs (vs. 28.6 per cent at Kent Island) and an 80 per cent loss of chicks (vs. 48.5 per cent at Kent Island). With an average clutch of three eggs this heavy mortality would result in a net production of about 0.5 fledgling for each pair of adults or, in other words, only a maximum of 39 per cent of the required productivity as calculated from the life table.

Paludan believed that fledgling production nearly as low as that observed in the Danish population would be sufficient to maintain the population if certain deficiencies in the life table were corrected. He reasoned that the number of birds which breed for the first time should equal the number that die during that year. From the life table he found the mean annual mortality from the second year onward to be about 15 per cent. This would mean that in a population of 1,000 birds, 150 would die during the year and 150 should begin to breed for the first time, if the population is to remain stable. Using the life table figure of 62.3 per cent mortality for the first year and 15 per cent mean annual mortality thereafter, he calculated a production of approximately 600 fledglings per 1,000 adults (1.2 per pair) would be necessary to yield about 150 birds two and a half years later, when he thought breeding began. This would require more than twice as many survivors as he had observed (0.54 per pair). However, Paludan reasoned that the observed first year mortality rate was higher than it should be owing to bias in favor of recoveries near the breeding colonies; a reduction in the first year mortality would increase the number of birds surviving to breeding age and, hence, reduce the required production of fledglings per pair. Also, he believed the prefledging mortality that he had recorded was in excess of that which is normal in Denmark. He concluded that the yearly production of between 0.5 and 1 fledgling per pair of adults would be sufficient to maintain the population, and even allow for the general increase that had been noted throughout Europe.

One significant probable error is the assumption that the entire population begins to breed in the third year. As we have seen above, a few gulls (20 per cent) do breed this early, but the average age is somewhat in excess of the fourth year. When Paludan's statistics are adjusted for this later breeding age, it is found that a pair of gulls would have to produce roughly 1.4 fledglings, rather than 1.2 fledglings.

TABLE VI

Life Table for Danish Gulls, Utilizing Kent Island Prefledging Data and Assuming First Year Recoveries to be Half of Those Actually Recorded (see p. 508 for explanation)

x	l_x	d_x	$1{,}000\, q_x$	e_x
0-0.07	1,000.0	286.0	286.0	1.43
0.07-0.19	714.0	346.3	485.0	1.92
0.19-1.10	367.7	166.6	453.0	3.56
1.10-2.10	201.1	43.8	217.8	5.37
2.10-3.10	157.3	30.0	190.7	5.73
3.10-4.10	127.3	19.9	156.3	5.96
4.10-5.10	107.4	14.9	138.7	5.97
5.10-6.10	92.5	16.0	173.0	5.85
6.10-7.10	76.5	9.6	125.3	5.97
7.10-8.10	66.9	11.2	167.4	5.75
8.10-9.10	55.7	9.1	163.4	5.81
9.10-10.10	46.6	7.5	160.9	5.85
10.10-11.10	39.1	3.2	81.8	5.88
11.10-12.10	35.9	7.5	208.9	5.36
12.10-13.10	28.4	2.2	77.5	5.64
13.10-14.10	26.2	3.2	122.1	5.07
14.10-15.10	23.0	3.8	165.2	4.71
15.10-16.10	19.2	3.2	166.7	4.54
16.10-17.10	16.0	4.3	268.7	4.35
17.10-18.10	11.7	1.1	94.0	4.77
18.10-19.10	10.6	1.1	103.8	4.22
19.10-20.10	9.5	1.6	168.4	3.65
20.10-21.10	7.9	0	0	3.29
21.10-22.10	7.9	1.6	202.5	2.29
22.10-23.10	6.3	3.7	587.3	1.73
23.10-24.10	2.6	0	0	2.50
24.10-25.10	2.6	0	0	1.50
25.10-26.10	2.6	2.6	1,000.0	.50

If normal fledgling production in the Danish population is assumed to be one per pair of adults, which is the maximum suggested by Paludan, it is necessary for the first year mortality to drop from the observed rate of 62.3 per cent to approximately 52 per cent, in order to replace the 15 per cent loss of breeding birds. This requirement seems reasonable if, as believed by Paludan, there was a disproportionately high recovery of first-year birds in the sample.

It is instructive to note (Table VI) that if the production of fledglings is assumed to be the same as at Kent Island (0.92 young per pair of adults) and if the recovery of first year gulls is halved, the first year mortality rate would be 45.3 per cent, which is almost exactly that found at Kent Island.[1] At sexual maturity there then would be nearly 64 pairs of birds, with a life expectancy of almost six years. If these birds laid an average of 2.5 eggs per clutch, there would be produced about 950 eggs, or nearly sufficient production to maintain the population. If there were three eggs per clutch there would be a net production of about 1,140 eggs, adequate productivity to permit about a five per cent annual increase in fledged birds.

From these calculations one is tempted to conclude that Paludan's first-year recoveries were twice as abundant as they would have been had the birds dispersed as widely as they do in succeeding years and that Paludan was correct in suggesting that breeding pairs need produce only about one fledged chick per year. However, there are certain peculiarities in the recovery data that require examination.

Paludan (1951, Table 29, pp. 108-109) presents a convenient tally of the annual recoveries for the year classes from 1917 through 1942. These records, in contrast to the Kent Island data, show extremely wide annual variations. For example, in the first year after banding the percentage of the total banded birds recovered ranged from 1.0 per cent in 1939 to 26.7 per cent in 1929, and in the second year the range was from 0 in five year classes to 4.0 per cent in 1937. Doubtless some of these great fluctuations are caused by sampling vagaries owing to the small number of birds banded each year and also to wide variations even within these small numbers (15 to 1,291 bandings per year). Nevertheless, there would seem to be some fluctuations which cannot be dismissed as sampling errors. These are well illustrated

[1] For these calculations it is necessary to assume that the Danish records begin on 1 July and that the first year recoveries are made in nine-tenths of a year, and thus are comparable with the Kent Island data.

by the second year recoveries for the year classes of 1935, 1940, 1941, and 1942, years in which the number of birds banded did not differ greatly. The number of gulls banded in these years was 765, 811, 861, and 710, respectively, and the number of second year recoveries, in the same order, were 0, 11, 1, and 1. Expressed differently, the recovery rates were 0, 1.36, 0.12, and 0.14 per cent.

We need not know the reasons for these fluctuations to appreciate what profound effects they have on a demographic study. The life table constructed by Paludan shows a mortality rate in the second year of nearly 22 per cent, a rate, as has been pointed out, considerably lower than that recorded for any other population. This rate was obtained from data which indicate that about 0.77 per cent of all Danish recoveries were made in the second year. This is the average for all 26 year classes. If, however, we eliminate the year classes for which there were no recoveries during the second year the average rises to 0.96 per cent. Using this figure in the life table would increase the second year mortality rate to 27.6 per cent, and if we employ the figure of 1.36 per cent, which is the percentage of second year recoveries in 1940, the mortality rate rises to nearly 35.8 per cent, which is almost exactly that of the Kent Island population. Concomitant with these increases in the second year mortality rate are decreases in that of the first year, so that in the early intervals the Danish life table becomes quite similar to that of Kent Island.

These calculations should suffice to illustrate that the Danish life table is based on small and highly variable samples, and that even seemingly minor changes in the data may have large-scale effects. This should also warn against assuming that Paludan's life table is more nearly correct than others merely because it "balances" when certain data are borrowed from other populations.

The second life table for European gulls is that prepared by Olsson (1958), for 1,222 recoveries, including those shot (60 per cent), from about 12,700 birds banded in Sweden, Norway, and Finland (=Fenno-Scandia) from the mid-1920's to the mid-1950's (Table VII). The average rate of recovery was about 9.5 per cent, which is nearly three times that at Kent Island and about ten per cent higher than that in Denmark. The table starts on August 1 following hatching. The oldest recovery is a gull in its 17th year; the oldest potential recovery at the time the study ended would be an individual in its 29th year. The raw data have been adjusted to compensate for the fact that some year classes had not been banded long enough to yield all their potential recoveries. It may be seen (Table IV) that the first year mortality of 56.8 per cent is somewhat lower than that found in Hickey's North American and Paludan's Danish populations, and that the second year rate is slightly higher than that of the North American gulls, and considerably higher than that of the Danish birds, but still not so great as that of the Kent Island population. For the next ten years the mean annual mortality is 33.8 per cent, which is more than twice the rate recorded by Paludan and moderately higher than that of the American and Kent Island populations.

Olsson had no records of the fledgling production in the Fenno-Scandian colonies and did not, therefore, attempt to test the accuracy of his life table against such data. Using the method devised by Hickey, it is found that 2.86 fledglings must be raised to

TABLE VII

Life Table for Fenno-Scandian Gulls Banded 1925-1935 (1,122 Recoveries) (Olsson, 1958)

x	l_x	d_x	$1{,}000\ q_x$	e_x
0–1	1,000	568	568	1.93
1–2	432	138	319	2.80
2–3	294	81	276	2.88
3–4	213	66	310	2.79
4–5	147	45	306	2.81
5–6	102	24	235	2.83
6–7	78	26	333	2.55
7–8	52	15	289	2.58
8–9	37	11	297	2.42
9–10	26	6	231	2.23
10–11	20	11	550	1.75
11–12	9	5	556	2.28
12–13	4	0	0	3.50
13–14	4	0	0	2.50
14–15	4	2	500	1.50
15–16	2	0	0	1.50
16–17	2	2	1,000	0.50

August 1 by each pair of breeding gulls if the population is to remain static. Even with a mean clutch of three eggs, such a high rate of nesting success appears improbable and it must be concluded that the Fenno-Scandian life table is also inaccurate.

POSSIBLE ERRORS IN THE KENT ISLAND TABLES

From the fact that the Kent Island colony was observed to have maintained its size from at least 1935 to 1948 (see p. 501) it seems reasonable to conclude that the population was either relatively stable during the 1930's and 1940's or, even more likely, that it was increasing and its surplus overflowed the colony and added to the expanding North American population. The life tables, however, indicate that the population should have been decreasing at a catastrophic rate. If we assume that the life tables are deficient, we must look for a source, or sources, of error within the data used in constructing the tables.

There are three kinds of error which might distort the life tables, causing them to indicate that the population was rapidly declining. First, banding recoveries may have been accumulated for too short a period (23 through 28 years), thereby failing to cover the full life spans of the six cohorts studied. Second, the 1947 egg and prefledging mortality rates, which were used in constructing the initial intervals of all six tables, may have been uncharacteristically high. Third, bands may have been recovered more readily in the early postfledging years than later in the life spans, causing an apparent increase in the mortality rates for the early intervals of the tables.

The first hypothesis, i.e. that a study allowing for recoveries for a maximum period of between 23 and 28 years does not cover the full life span of the Herring Gull, is correct, but probably only to a small and insignificant degree. For example, a Kent Island gull has been found alive in its twenty-sixth year, and a bird banded as an adult was recovered 24 years later meaning it was a minimum of twenty-seven years old when it died. There are also records of captive Herring Gulls which have lived nearly fifty years (Gross, 1940); it is conceivable that some wild individuals may attain an equally advanced age. Nevertheless, it seems that very few gulls live beyond their twenty-third year, which is the oldest potential recovery within the youngest cohort studied at Kent Island, and those birds that do live longer doubtless have little influence on the reproductive rate of the population because of their relatively insignificant numbers and possibly (unproven) because of sterility brought about by senility.

Support for the argument that the life tables adequately cover the life spans of the gulls may be found in the recovery data. Of the 954 recoveries from the five oldest cohorts, with a maximum potential age ranging from 24 to 28 years, only one individual (0.16 per cent) reached the age of 24, none exceeded that, and but three lived more than 18 years. Expressed differently, less than one-fifth of one per cent of the recoveries were of birds older than 18 years. In Paludan's Danish study (1951) there were eight cohorts with a maximum potential age between 26 and 34 years. Of the 236 recoveries from these cohorts there was just one bird in its twenty-sixth year and the recovery rate between the eighteenth and twenty-sixth year was only 0.8 per cent of the total sample. The maximum potential age of birds in Olsson's (1958) Fenno-Scandian population was twenty-nine years, but the oldest recovery was a single seventeenth-year individual.

There is, of course, the possibility that a loss of bands could account for the failure to recover gulls even older than those now known. But it is believed that while the frequency of recoveries may be reduced because of band loss, there is little likelihood that the maximum span of life is significantly greater than that which has been recorded. We must, therefore, seek another explanation for the failure of the life tables to document the population dynamics of the Kent Island colony.

The second hypothetical source of error in the life tables, i.e. that the prefledging mortality in 1947 was unusually high, is almost certainly void. It was found that nearly 29 per cent of the eggs failed to hatch and about 48.5 per cent of the young died before fledging, resulting in 63.2 per cent mortality, or a net production of 0.92 fledglings per breeding pair (Paynter, 1949). This falls well within the range recorded at other Herring Gull colonies. For example, Paludan (1951) who admitted that his calculations are imprecise, estimated a production of 0.5 fledged young per pair, or 83 per cent prefledging mortality. In a study on the Summer Isles in the Irish Sea, Darling (1938) found five colonies (ranging from 6 to 150 individuals) which had prefledging mortality rates between 58.3 and 88.9 per cent, and which yielded from 0.78 to 0.96 fledged young per nest. Drost, Focke, and Freytag's (1961) German colony, which started with two pairs of birds and in 12 years built up to 139 pairs, had an average prefledging mortality rate of about 75 per cent, resulting in the fledging of an average of 0.7 gulls from each nest. On Skokholm, an island off the coast of Wales with a colony of 300 pairs of gulls, Lockley (1947) estimated that less than one fledgling per adult pair was produced. In another Welsh colony of 440 pairs, Harris (1964) reported a production of about one fledgling for each two nests.

Other species of gulls laying three-egg clutches show a similar range of nesting failures. A colony of Ring-billed Gulls (*L. delawarensis*) in Michigan suffered 88 per cent prefledging losses, producing 0.67 young per pair of adults (Emlen, 1956). The California Gull (*L. californicus*), in a colony in Utah, was found to have unusually low prefledging mortality, suffering a loss of only about 40 per cent of its eggs and young, and fledging 1.77 chicks per nest (Behle and Goates, 1957). In British Columbia a colony of Glaucous-winged Gulls (*L. glaucescens*), studied for two years, produced 1.0 and 1.7 young per nest, and had a mortality rate of 64 and 52 per cent, respectively (Vermeer, 1963). Four small colonies of Lesser Black-backed Gulls (*L. fuscus*) in the Summer Isles produced about 1.5 young from each nest, with a prefledging mortality rate of approximately 48 per cent (Darling, 1938).

In summary, the prefledging mortality rate at Kent Island in 1947 was below that which has been found in most other Herring Gull colonies and in a colony of *L. delawarensis*, and somewhat higher than that recorded for populations of *L. californicus*, *L. glaucescens*, and *L. fuscus*. From this it is concluded that the 1947 prefledging survival data are in the right order of magnitude and probably are not responsible for the failure of the composite life tables to indicate that the population was stable or increasing.

The third type of error that could distort the Kent Island life tables, causing the survival rates for breeding birds to appear too low to maintain the population, is a disproportionately high recovery of bands in early age classes. This could be brought about through some circumstance which allows young birds to be more readily recovered than older individuals, through a loss of bands among older birds which would reduce their rate of recovery, or through a combination of these factors. Both phenomena are difficult to detect but almost certainly at least one is the reason that the life tables are not reconcilable with the observed status of the population.

Paludan (1951, p. 111) believed that the mortality rate for the first year class of the Danish gulls was unrepresentatively high because newly fledged birds died near the natal colony, where they are more likely to be recovered and reported than older birds which range more widely. At Kent Island, however, the fledglings quickly leave the colony and winter far south of New Brunswick. Each successive year the length of the migration is lessened until as adults the birds winter only a few hundred miles from the colony (Gross, 1940). This migration pattern reduces the opportunity for any recoveries at Kent Island during the winter months. Moreover, the records indicate that very few immature gulls are recovered at the colony during any season. There seems no possibility that the recovery sample is biased in favor of immature birds because they die in the vicinity of the natal colony.

There remains to be considered the possibility that the wide dispersal of young birds during the winter, and their failure to return to the colony during the breeding season, might in some way enhance their chances of recovery over those of the less wide-ranging adults. If the immature gulls were in closer proximity than the adults to urban areas, where dead birds are more likely to be found, this possibility would exist. However, during the winter the younger birds are scattered from the heavily populated northeastern United States south to the more sparsely inhabited Gulf Coast and Central America, and in the breeding season return to the Northeast. On the other hand, the adults winter in the heavily populated Northeast and breed where observers are constantly alert for dead birds wearing bands. Bias in favor of the recovery of immature gulls seems improbable under these circumstances.

Having considered and rejected as improbable all other potential sources of error, we are left with only band loss to account for the discrepancies between the life tables and the observed status of the Kent Island colony.

All Kent Island gulls were marked with aluminum butt-end bands, rather than with the locking, clip-type bands now used in Europe. In a British study, using butt-end and clip bands on different samples plus supplementary durable plastic bands, Poulding (1954) found that during the first year after banding as fledglings, Herring Gulls with locking bands were recovered with twice the frequency of birds wearing butt-end bands. Breaking down the analysis further, it was noted that when the gulls wore butt-end bands only about four per cent of the year's total recoveries were made in the second half of the year, whereas nearly 41 per cent of the recoveries occurred in the second six months when the birds wore clip-type bands. Thus the data indicate that 50 per cent of the butt-end bands are lost in the first year and nearly all of this loss takes place before the bands are six months old. Observations of living birds confirmed the 50 per cent loss of butt-end bands and showed a complete retention of clip bands.

This evidence strongly suggests that the heavy initial loss of butt-end bands may be caused by the removal of the bands by the gulls, rather than by a weakening of the bands through wear. Differences in the strength of individual bands, and possibly variations in the manner of closing them, could well account for the rapid loss of half of the bands while some of those in the remaining half are retained in good condition for many years.

If this type of band loss occurs among Kent Island birds, the life tables would be significantly affected. It would mean, disregarding for the moment the normal reduction in the size of cohort caused by death, that at the time of fledging the banded sample would be twice the size it is when entering the second year of life. It follows that the number of recoveries in the second year, and all subsequent years, would be half of the total had there been no loss of bands and that the recoveries in the first year would be somewhat lower, but not a full 50 per cent lower because the bands are retained for part of the first half year. Viewed from a different aspect, recoveries in the first year would be disproportionately more numerous than those of the remaining year classes. The effect on the life table would be a reduction in the calculated number of birds surviving beyond the first year and, of course, a marked decrease in the apparent number of individuals which survive to the breeding age.

We have no evidence that Kent Island gulls lose half their bands during the first six months, but if we adjust the life table to compensate for such a loss and the table is then reconcilable with the apparent true status of the population, we shall have good circumstantial evidence that this is the source of error. If, for the sake of simplicity, we assume that the mortality rate is constant during the entire first year and that 50 per cent of the bands are lost at the end of the first six months and none in the second half year, one-third of the recoveries would occur in the second six-month period. Doubling this figure will give the number of recoveries which would have been made if the initial banded sample had been half its original size and there was no subsequent loss of bands. For the six combined cohorts there were 1,099 recoveries, 494 of which occurred during the first year. Making the proposed adjustments for the first year, the first year recoveries would drop to 329 and the total for the entire life span to 934.

Using these data to construct a new life table, it is found that the number of survivors reaching the breeding age of year 3-4 rises to about 116, versus 98.4 in the uncorrected table. The life expectancy at this age remains 3.3 years. With a breeding cohort of this size and with this life expectancy, a total of 477 eggs could be produced, which is an increase of 71 eggs over the total (406) calculated for the uncorrected life table. Nevertheless, this is still less than half the number required to maintain a level population.

If we were to assume that early band loss is the sole source of error in the life table, in order to achieve sufficient production at the breeding stage it would be necessary to adjust the recoveries in the first year so that their total would fall well below that of the second year. Such a low rate of mortality is obviously spurious. We must conclude that while early band loss is a distinct possibility in the Kent Island population, there must be additional losses later in the life span.

Band loss may fall into three broad patterns. The first, and the most expected, is loss which is correlated with the age of the bands. One would expect bands to become progressively weaker through wear and as a result be lost with increasing frequency. The second type is a proportional, or constant, loss. This is most likely to take place if the bands are continually removed by the birds or if they merely drop off at random. The third pattern, which may be uncommon, is an inconsistent, or fluctuating, loss. This may occur because of variations in behavior, such as shifts in feeding ranges from less saline to more saline water, which might have a variable effect on the durability of the bands, or because the new bands are not of uniform strength or are not all fastened securely. The large initial loss of bands noted by Poulding (1954) is an example of an inconsistent pattern which seems attributable to the latter cause.

If we are able to determine the pattern of band loss among Kent Island gulls it may then be possible, in certain instances, to adjust the raw data to compensate for the losses and to construct a life table which will document the colony's demography. Because the Kent Island birds were all marked with similar bands there is no control group against which the various cohorts may be tested, as in Poulding's study. We must, therefore, see if any evidence of band loss may be detected within the data available. Semi-logarithmic graphs of survivors (l_x) offer a means of approaching the problem.

If survivors (l_x) are plotted against age on a semi-logarithmic graph, the points will form a straight line if the rate of survival is constant. If the survival rate should decrease, or if there is an accelerating loss of bands which would create an apparent decrease in the rate of survival, the line will assume a sigmoid shape, being deflected downward. As may be seen in the plot for the six combined cohorts at Kent Island (Fig. 2), starting with the fourth year (year 3-4) of life, the survival rate is relatively constant for at least ten years (to year 12-13). There is then a downward trend, but there are so few recoveries one cannot be certain that the pattern is not an artifact. From this it is evident that if there is band loss that is correlated with age, it does not begin until sometime after age thirteen, by which time the cohort has dwindled to a small fraction of its initial size.

A further test for a correlation between a loss of bands and the time which they have been worn may be made by utilizing the recoveries of birds banded as adults. Between 1936 and 1947 a total of 1,856 gulls in adult plumage were banded; 97, or 5.2 per cent, were recovered up to 30 June 1963 (Table VIII).

TABLE VIII

Kent Island Adults Banded and Admissible[1] Recoveries

Year	Banded	Recoveries	Per cent
1936	200	2	1.00
1937	196	13	6.63
1938	611	46	7.53
1939	100	5	5.00
1941	155	5	3.23
1946	497	21	4.22
1947	97	5	5.15
Total	1,856	97	5.23

[1] See p. 493 for definition of admissible recoveries.

Nothing is known of the ages of these birds beyond the fact that they were in adult plumage and, therefore, were at least in their fourth year of life when banded. The maximum time available for recoveries from the youngest cohort is 16 years and from the oldest cohort it is 28 years. The oldest recovery was a bird banded 24 years earlier; the next oldest were two gulls which had borne their bands for 14 and 17 years, respectively. A semi-logarithmic survivorship curve for the 97 recoveries from the combined seven cohorts is shown in Figure 3. Owing to the paucity of older recoveries, no adjustment has been made for the fact that after age 16 the number of potential recoveries decreases because not all cohorts have been banded sufficiently long to yield recoveries between ages 17 and 24.

In Figure 3 a comparison is made between the semi-logarithmic survivorship curve for the birds banded as adults and the curve, starting at the fourth (adult) year, for those gulls banded as fledglings. If there is a positive correlation between the age of the bands and their loss, one would expect the survival rate for the latter group to decrease, and the curve to become deflected three years sooner than for the former group, because the birds banded as fledglings had borne their bands three years longer. If band loss begins during the first year following banding, the curves would diverge immediately. If it starts some years later the two lines would remain parallel until band loss begins, when the curve for the group with older bands would descend more rapidly; the plot for the group with the newer bands would continue in a straight line (a constant annual survival rate) for three additional years and then it too would begin to fall away.

As may be seen in Figure 3, the two curves remain nearly parallel for ten years, or in other words, until the group banded as fledglings has reached its thirteenth year. Then, as has been discussed, the curve for the group with the older bands begins to decline at a more rapid rate. This is not followed three years later by a decline in the other curve, which one would expect if bands began to be lost at an increasing rate after they had been worn thirteen years. In both groups, and particularly in the group banded as adults, there are so few recoveries in the older age categories it would be imprudent to attempt at this time to read any significance into these differences. All we may safely conclude is that if band loss is a function of age it almost certainly does not begin until the bands have been worn at least thirteen years. Because this means that the birds could have bred for ten seasons prior to the beginning of accelerated band loss, there seems little likelihood that this type of band loss would have a significant effect on the life tables.

This test also reveals an interesting fact regarding early band loss. It indicates that gulls banded as adults do not suffer a greater loss of bands in the first year than in later years, which is contrary to what one would have expected from Poulding's study (1954) of British fledglings. This is probably an indication that the North American butt-end bands are more uniformly durable than the British butt-end bands. This also seems to explain why the attempt to compensate for disproportionately

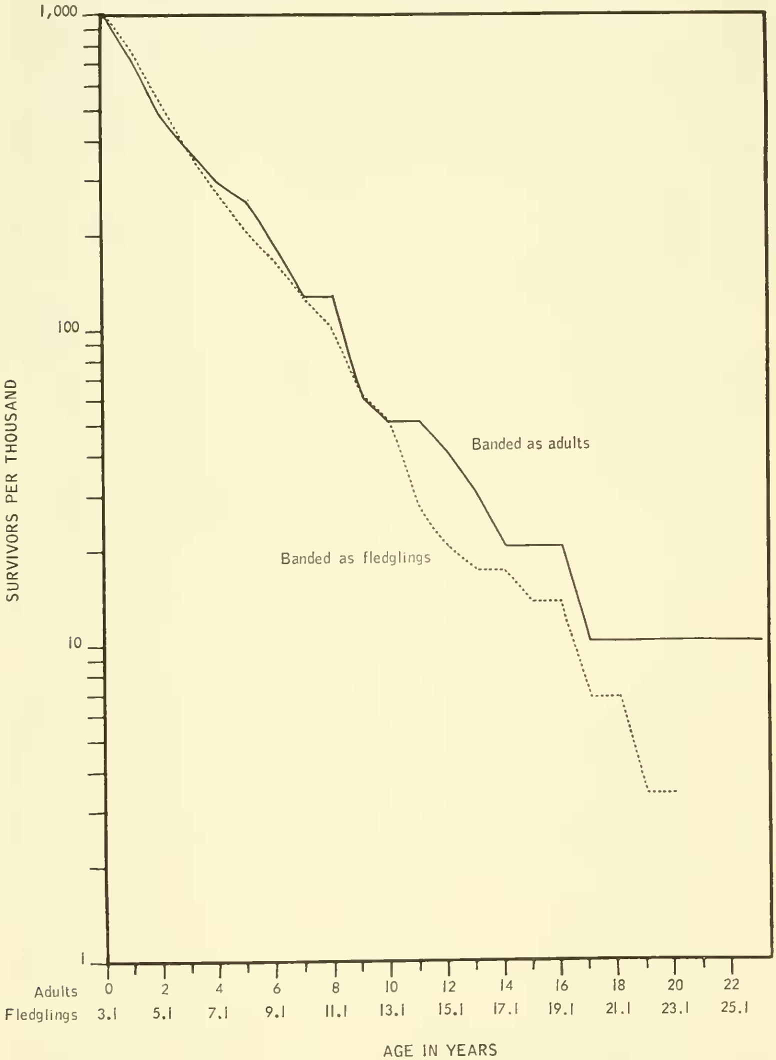

FIG. 3. Survivorship curves for Kent Island gulls banded as fledglings and as adults.

heavy band loss within the first year class of Kent Island gulls, banded as fledglings, failed to produce a satisfactory life table. Nevertheless, one could argue that adults do not remove their bands with as great a frequency as fledglings, explaining this difference by assuming that the legs of fledglings are more sensitive than those of adults and that the irritating bands are removed. Or, possibly, one could reason that in the process of learning to detect what is food, and what is not, the fledglings are attracted by the shiny bands and peck at them until they are loosened and lost. However, the fact that the Kent Island life table is not appreciably improved by adjustments made to compensate for heavier band loss in the first year of life seems to negate such arguments. The simple explanation that British butt-end bands are of more variable durability than those used at Kent Island seems the most satisfactory explanation.

The only pattern of band loss yet to be considered is that which occurs at a constant, i.e. proportional, rate. Having concluded that band loss is not positively correlated with the age of the band, and that bands are not lost with a greater frequency at any particular time during the bird's life, it is almost certain that the Kent Island population suffers a steady loss of bands during its entire life span. This would progressively reduce the number of recoveries in each successive age interval, thereby depressing the survivorship curve and reducing the calculated expectation of life throughout the life table.

We do not know the rate at which bands are lost and whether this rate is sufficiently low to allow at least a portion of the population to retain its bands until it has lived its full life span. However, because a living gull was found at Kent Island which had borne a band for 26 years, and because there are records from there of four birds which died between the ages of 20 and 24, it is evident that the rate of band loss must be comparatively low. For example, if the annual loss ran as high as 20 per cent, the roughly 32,000 individuals in the Kent Island sample would have dwindled to about 455 banded birds by the beginning of the twentieth year, even without considering attrition owing to mortality. If the average annual mortality were 10 per cent, making a cumulative annual reduction in the marked population of 30 per cent, there would have been just 37 banded survivors at the start of the twentieth year, certainly too few to have yielded five records of birds 20 years and older. Assuming that losses and mortality are each 10 per cent annually, there would be approximately 445 banded survivors after nineteen years, or about 1.4 per cent of the initial sample, which *seems* ample to allow for the recovery of five individuals in the next seven years. Although the Herring Gull is a long-lived species, 10 per cent average annual mortality would appear rather low; Drost et al. (1961) calculated a rate of 10 per cent for adult birds, but our calculations must include immatures within the average. If we continue to allow for 1.4 per cent survival at age 20, any increase in the mortality rate would have to be balanced by a decrease in the rate of band loss. Thus, 15 per cent annual mortality, which is about the figure found by Paludan for birds between the ages of 2 and 12, would mean a band loss of five per cent at the most. Crude as these calculations may be, it seems reasonable to conclude that Kent Island gulls lose bands at an average rate somewhere in the vicinity of 5 or 10 per cent per year and that the average annual mortality rate must range between 10 and 15 per cent.

These speculations are based on the premise that bands are recovered throughout the life span of the birds and are not totally lost before the oldest gulls die. There can be no proof that this is correct, but empirically it would seem that the oldest recoveries probably very nearly represent the potential natural longevity of the Kent Island Herring Gull. A larger cohort, more durable bands, and additional decades of observation surely would produce recoveries older than those now known, but it is difficult to imagine that these could be more than an insignificant fraction of the total sample.

CONCLUSIONS

It is now evident that a continued loss of bands accounts for the failure of the Kent Island life tables to reconcile with the observed status of the population (i.e. either a stable or increasing population). Unfortunately, in spite of our estimate that the loss amounts to about 5 or 10 per cent annually, there is no way by which the raw data may be adjusted to compensate for these losses. We know, for example, that there were 494 recoveries for the combined cohorts in the first nine-tenths of a year, and that without a ten per cent loss of the banded sample there would have been about 549 recoveries. In the second year there were 220 recoveries, but this number, without band losses during the second year, would have been approximately 243, plus an unknown number of individuals which lost bands in the first year but survived to die during the second year. The difference between the recorded recoveries and the number of recoveries there would have been had there been no band loss, increases, of course, in each successive age interval. This also has the effect of accelerating the descent of the survivorship curve and probably accounts for the difference between the Kent Island curve and that of the Danish population (Fig. 2).

From this analysis we must conclude that because of band losses the Kent Island banding records are nearly valueless as a means of investigating the dynamics of this population of Herring Gull. Their only use in studies of this sort, if one is willing to accept the premise that some bands are sufficiently durable to be retained through the life span of at least a few of the longest living gulls, is to demarcate the maximum potential longevity of the species. All North American Herring Gulls have been marked with similar butt-end bands, and band loss is without doubt the reason Hickey (1952) also failed in his attempt to construct an accurate life table. Because aluminum butt-end bands are used on almost all birds banded in North America, any data obtained from this source is suspect. Future workers should be particularly alert to the possibility of band loss before investing time and effort in this type of research.

Locking bands were used on nearly all gulls banded in Fenno-Scandia (Olsson, 1958). However, the material used in the manufacture of the bands evidently was not very durable, for Olsson estimated that about 5 per cent of their original weight was lost annually. Such rapid wear, and the resulting loss of bands, is presumably the reason for the apparent reduced maximum longevity of the Fenno-Scandian gulls when compared with North American and Danish birds. There can be little doubt that the similarity between the survivorship curves for Fenno-Scandian and North American birds is caused by band losses.

Paludan (1951) does not mention the type of band used on Danish gulls, but, according to Poulding (1954), butt-end bands were first used and later abandoned in favor of locking bands. Possibly some of the yearly variations in recovery rates that have been noted (p. 510) are attributable to changes in the type of bands employed. Nevertheless, this cannot be one of the main causes for these variations because one would expect the recovery rates for the more recent year classes to be consistently higher than those for the older year classes, but no such pattern is evident.

Band loss almost certainly occurred in the Danish population. Even if locking bands eliminate losses early in the life span, wear surely accounts for band failures in the later years of this long-lived gull. Bias in favor of recoveries during the first year of life, and band losses during the latter part of the life span, must be the primary reasons for the deficient Danish life table and its dissimilarity to other life tables. Fundamental differences between the mortality rates of the North American and Fenno-Scandian populations, on one hand, and the Danish population, on the other hand, as proposed by Paludan (1951) and Olsson (1958), seem most unlikely.

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SUMMARY

1. At Kent Island, New Brunswick, 31,694 Herring Gull (*Larus argentatus smithsonianus*) fledglings were banded with aluminum butt-end bands between 1934 and 1939; by 30 June 1963 there were 1,099 (3.47 per cent) recoveries suitable for use in a mortality series (Table I).

2. The maximum potential age for a recovery in the oldest cohort is 28 years, and in the youngest cohort it is 23 years; the two oldest birds at death were in their twenty-fourth and twenty-second years; one gull was captured alive in its twenty-sixth year.

3. About five per cent of all recoveries are of birds which have been shot; rates vary within the six year classes from 3.6 to 6.5 per cent; probably more birds are shot than are reported because the species is protected by law; no gull older than thirteen has been reported shot; there is no indication that immature birds are more readily shot than adults.

4. Using prefledging mortality data for 1947 (Paynter, 1949), composite life tables are constructed for each of the six cohorts and for the combined cohorts (Table II); survivorship curves

are also drawn (Figs. 1 and 2); there are minor yearly variations, but the patterns are generally similar, showing heavy mortality the first year, lessened mortality the second year, and a lower, relatively constant, rate thereafter.

5. Assuming breeding begins in the fourth year (year 3-4), that the average clutch is 2.5 eggs, and that each nesting results in the production of 0.92 fledglings (Paynter, 1949), it is found that an average of about 98.4 gulls attain breeding age from each 1,000 eggs laid, and these have a life expectancy of 3.3 years, enabling them to produce 405.9 eggs, or about 41 per cent of the number required to maintain a stable population.

6. The population is believed to have been stable, or possibly expanding, from at least 1935 to 1948. The life tables must, therefore, be faulty.

7. Three types of error leading to distorted life tables are possible: 1. recoveries were accumulated for too short a period (23 to 28 years) to document the potential life span; this is probably a minor and insignificant source of error. 2. The 1947 egg and prefledging mortality rates were excessively high; this is rejected because comparable rates have been found in this and related species. 3. There is a disproportionately high recovery of bands in the early age classes because (a) young birds are more readily recovered, (b) older birds lose bands and are lost from the sample, or (c) both factors are operative.

8. It is certain that band loss, resulting in a disproportionately high recovery of young birds, must account for the failure of the life tables to document the demography of the Kent Island population.

9. Band loss could be (a) positively correlated with the age of the band, (b) proportional (i.e. constant) with respect to the size of the sample, or (c) fluctuating; it is concluded that bands are lost at a relatively constant rate throughout the life span.

10. Assuming that some bands are retained long enough to document the maximum potential life span, mortality and band loss combined seem not to exceed 20 per cent annually; it is suggested that band loss averages around 5 or 10 per cent per year and that the average annual mortality ranges between 10 and 15 per cent.

11. Hickey's (1952) life table (Table III; Fig. 2) for North American gulls proved faulty presumably because of band losses similar to those at Kent Island.

12. Olsson's (1958) life table (Table VI; Fig. 2) for Fenno-Scandian gulls is similar in pattern to those for North America

and Kent Island; locking bands probably eliminated losses through mechanical failure, but rapid wear (five per cent annually) doubtless resulted in band loss correlated with age and eventually to a total loss of marked birds by the eighteenth year, foreshortening the apparent maximum life span.

13. Paludan's (1951) life table (Table V; Fig. 2) for Danish gulls, with its higher survival rate, most nearly fits what is known of the demography of the species but bias in favor of recoveries during the first year, wide variations (of unknown cause) in yearly recovery rates, and probably band losses toward the end of the life span distort the data.

14. Suggestions of essential differences between the mortality rates of the various populations are considered spurious.

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